Mitt. Bayer. Staatsslg. Paläont. hist. Geol.	38	209–225	München, 15. 12. 1998

Biomechanical Analyses of Rodent Incisors: A Morphological and Microstructural Adaptation

By Rahul Srivastava*

With 20 Figures

Abstract

3-D Finite Element Analyses (FEA) of rodent incisors suggest that under the gnawing load conditions, chisel shaped incisors maximally reduce the magnitude of the stresses.

The study and analyses suggest that worn dentine and Hunter Shreger Bands (HSB), and presence of only radial enamel on cutting edge minimises wear. The tensile stresses due to gnawing load were noticed mainly in Y and Z directions i.e. in the directions of the enamel width and the thickness in rodent incisors.

The confirmatory results were obtained through laboratory experiments using Universal Testing Machine (UTM) by loading recent rodent incisors.

The orientation of the HSBs in Y and Z directions of the incisors' enamel prevent hairline cracks due to the gnawing stresses. This adaptation has been found to be least developed in the pauciserial enamel pattern present in Eocene rodents and better developed in the multiserial and the uniserial enamel pattern respectively, present in the rodents of Oligocene – Recent age.

Kurzfassung

Die dreidimensionale Finite-Element-Analyse (FEA) von Nagetierincisiven legt den Schluß nahe, daß unter dem Belastungsdruck während des Nagens meißelförmige Schneidezähne die Magnitude der Spannung am stärksten reduzieren.

Die Analysen und Untersuchungen zeigen, daß abgenutztes Dentin und Hunter-Schreger-Bänder (HSB) und das Auftreten von ausschließlich radialem Schmelz auf der Schneidekante die Abnutzung minimieren. Die Zugspannungen während der Belastung beim Nagen wurden vor allem in Y- und Z-Richtung beobachtet, das heißt in Richtung der Breite und Stärke der Incisiven.

Die Bestätigung dieser Ergebnisse wurde durch Laborexperimente mit einer „Universal Testing Machine" (UTM) erhalten, die mit rezenten Nagerincisiven beschickt wurde.

Die Orientierung der HSB in den Y- und Z-Richtungen des Incisivenschmelzes verhindert Haarrisse durch den Kaudruck beim Nagen. Es wurde festgestellt, daß diese Anpassung in dem pauciserialen Schmelzmuster der eozänen Nagetiere weniger gut entwickelt war als in dem multiserialen oder uniserialen der Nagetiere vom Oligozän bis heute.

---

* Rahul Srivastava, Department of Geology, Lucknow University, Lucknow, India, Present Address: Fuhlrott Museum, Auer Schulstrasse 20, 42103, Wuppertal, Germany

Introduction

Skeletal tissues provide the physical and protective supports for the soft tissues and play an important role in counter balancing any loads/stresses in specific directions. Mammalian dental enamel demonstrates the same function as it takes most of the chewing load/stress coming on occlusal plane. In the present paper the focus has been on the rodent incisors for the simple reason that these slender structures (approximate diameter 2-3 mm) have enormous strength and wear resistance. They are easily obtainable and can be studied in terms of functional importance through time i.e. in an evoutionary series.

Scanning Electron Microscope (SEM) studies of mammalian dental enamel have showed various kinds of enamel microstructure in different groups of mammals. This variation is mainly due to the difference in the arrangement of enamel prisms which are the bundles of the fibres of apatite crystallites (Boyde et al., 1988; Pfretzschner, 1988).

In rodent incisors, the enamel is an outer layer which covers the dentine only on the buccal side. The HSBs occupy the inner half (Portio Interna, i.e. towards the Enamel-Dentine Junction : the EDJ) of the total enamel thickness. The outer enamel (Portio Externa) lacks HSBs and instead there is radial enamel in which the long axes ('C' axis) of the enamel prisms are oriented radially from the EDJ as seen in a horizontal plane (Koenigswald & Clemens, 1992).

The HSBs are interpreted as strengthening devices which prevent the propagation of hairline cracks at higher load conditions (Koenigswald, et al., 1987). The arrangement of the HSBs and the enamel microstructure vary in different groups of mammals and are closely related to the shape related functions of the teeth (Koenigswald & Clemens, 1992). The rodent incisor enamel possesses the most derived and complicated microstructure among all the mammals (Koenigswald et al., 1987).

The microstructure and functional morphology of rodent incisor enamel has been studied in detail by many workers (Tomes, 1850; Korvenkontio, 1934; Boyde, 1976; Wahlert, 1989; Sahni, 1980; Koenigswald, 1985, Flynn, 1987 and recently by Martin, 1993). The work of Tomes (1850) was extended by Korvenkontio (1934), when he described three types of rodent incisor enamel microstructures: the pauciserial, the multiserial and the uniserial. This classification was based on the characteristics of the Hunter Schreger Bands (HSBs) in the inner enamel. Lately, Martin (1993) differentiated the rodent incisor enamel types, according to the distribution, inclination and the general regularity of the HSBs and the orientation of the Inter-Prismatic Matrix (IPM). In the pauciserial enamel, the HSBs, arranged perpendicular to the EDJ, are 2-6 prisms wide with an irregular bifurcation of the bands and the crystallites of the IPM are arranged parallel to the prisms, and transition zones of prisms between the HSBs are lacking (Sahni, 1980 and Martin, 1993). This kind of enamel pattern is characteristic of the extinct families of Eocene age; most of the ischyromyoids, anomaluroids and ctenodactyloids possess pauciserial enamel (Martin, 1993). In the multiserial enamel, the HSBs are 3-6 prisms wide and are inclined to the EDJ (Sahni, 1980). The orientation of the IPM diverges in the multiserial and well defined transition zones are present between the HSBs (Martin, 1993). In the uniserial enamel, the HSBs are one prism wide and are inclined to the EDJ; the IPM is oriented approximately at 90 degree and transition zones are evident between the HSBs (Sahni, 1980; Koenigswald, 1985; Martin, 1993). The rodent families of Oligocene - recent age are characterised by the multiserial (present in most of the phiomorphs, caviomorphs) and the uniserial type of enamel pattern (present in most of the cricetids, sciuromorphs and myomorphs and few anomaluroids). The uniserial pattern is considered to be the most derived and the pauciserial is considered to be the most generalised type of enamel with an intermediate multiserial (Sahni, 1980; Martin, 1993).

In the present paper a functional interpretation of all the three types of incisor enamel was

undertaken. It was noticed that the uniserial enamel in comparison to the multiserial, provides better reinforcement structure to prevent the failure of the teeth under the gnawing load conditions. The pauciserial enamel was found to be the least effective to counter balance the gnawing stresses.

In the present work, 3-D Finite Element (FE) modelling and experimental load analyses in laboratory using Universal Testing Machine (UTM) have helped delineating the direction of principal stresses in the incisors of rodents, for better understanding of their functional significance in the light of their enamel microstructure as observed under the SEM.

Previous studies so far made contained no experimental evidences, in which the actual tooth is subjected to load to analyse the direction of the failure, though some shell models made up of glass-epoxy have been analysed in laboratory for load analyses (KOENIGSWALD et al., 1987; RENSBERGER, 1993, 1995a, 1995b), but no such analysis has been done so far for rodent incisors. Prior to these many models for conical teeth, herbivore molars were produced in 2-D plane using quadrilateral plate elements and shell elements (KOENIGSWALD, et al., 1987; PFRETZSCHNER, 1988, 1992; RENSBERGER, 1992 and MARX, 1995). The 2-D plate elements do not provide stresses in the direction which is not parallel to the elements i.e. in the direction of the thickness of the enamel. In the present study the 3-D hexa elements have been used to calculate the stresses in the rodent incisors. The 3-D analysis provides stresses in all the three orthogonal directions of the enamel i.e. along the length, the width and the thickness.

The FEA allows calculation of stresses in the objects of any shape and complexity. In FEA, the models are formulated as a series of connected subunits called elements of simple shape and size.

The computer modelling of gnawing events in rodent incisors have shown that the enamel of long curved slender incisor bear all the load coming nearly parallel to the incisal part of the tooth.

Material

To meet the objectives following material were used in the study:

For SEM Study:

1 Incisor fragments of ctenodactyloid rodents (Locality: Upper Subathu Formation, Metka, Rajauri District, J & K. Age: Middle Eocene, approx. 45 Ma).
2 Incisor fragments of murid rodents (Locality: Pinjor Formation, Upper Siwaliks, Moginand, Nahan District, H.P. Age: 2 Ma).
3 Incisors of *Cavia procellus* (Guinea Pig. Age: recent).
4 Incisors of *Mus musculus* (House Rat. Age: recent).

Dental elements of Eocene ctenodactyloid rodents, Plio-Pleistocene rodents (murids) were collected through maceration of the Upper Subathu and Siwalik rock samples already housed in Vertebrate Paleontology Laboratory, Panjab University, Chandigarh.

For Finite Element Study:

To understand the significance of curvature in rodent incisors and dissipation of stresses in a straight and a curved structure following models were used in the study :

1 Computer model of simple straight double layered bar/beam
2 Computer model of simple curved double layered bar/beam
3 Computer model of chisel shaped curved rodent incisor

For Laboratory Experiments:

1 Incisors *of Cavia porcellus* (Guinea Pig).
2 Incisors of *Mus musculus* (House Rat).

Methodoloy

For scanning electron micrographs, all the incisors were sectioned longitudinally. The sectioned teeth were ground, polished and the fossil teeth were etched with 5% HCl for 20 seconds, whereas recent teeth were observed after brief etching with Hydrogen-peroxide. These etched sections of the teeth were then coated with gold to make the surface conducting and were viewed under the SEM (JEOL JSM T-330, installed in the Department of Geology, Lucknow University) at various magnifications ranging between 35 - 5000 (accelerating voltage 15 kv).

The finite element modelling was done with the help of a FEA software LapFEA (2000 nodes version, native for Power Macintosh) on a Power Macintosh (6100/66) computer. For the FEA,

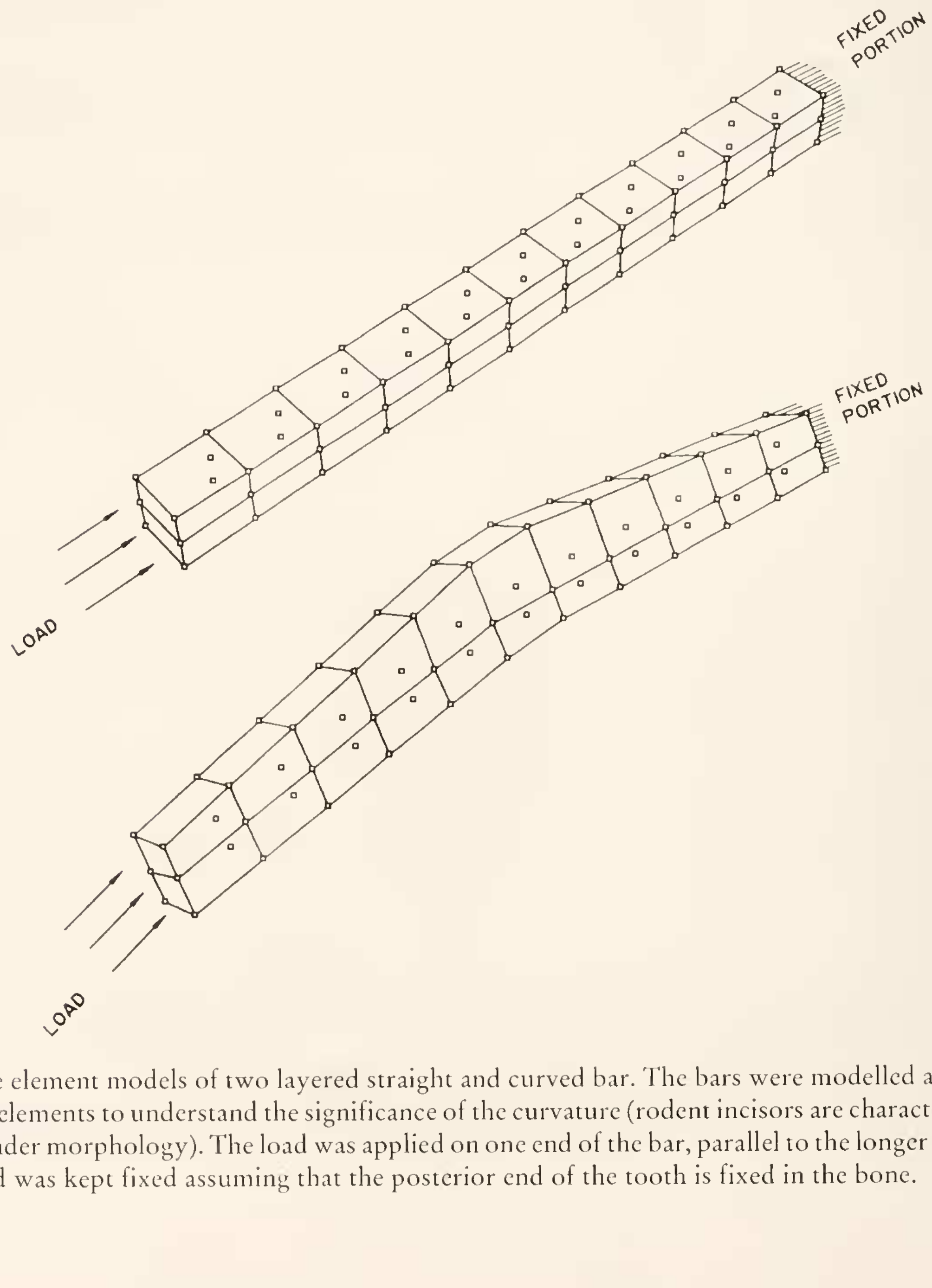

Fig. 1: Finite element models of two layered straight and curved bar. The bars were modelled as a series of 3-D hexa elements to understand the significance of the curvature (rodent incisors are characterised by a curved slender morphology). The load was applied on one end of the bar, parallel to the longer axis. The opposite end was kept fixed assuming that the posterior end of the tooth is fixed in the bone.

the bars/beams and the rodent incisors were modelled as a series of 3-D hexa elements (figs. 1 & 2)

While modelling the teeth for stress distribution study, the material was considered to be isotropic i.e. it has the same elastic modulus in every direction. In this assumption, error would be uniform and hence would not affect the comparison of the results. Enamel prisms may be orthotropic i.e. they may have different moduli of elasticity along the long axis of prisms in comparison to a direction perpendicular to them. Since, a small chunk of enamel consists of a number of prisms in diverse direction, hence it is not possible to calculate the Young's Modulus values for the dental enamel of different mammals excepting some insectivores (Rensberger, 1992). In the present work, for FEA, the Young's Modulus, Poisson's Ratio, Shear Modulus and Mass Density values of the enamel as a general were taken (Rensberger, pers. comm.; Waters, 1980).

Young's Modulus (Stress/Strain) = 0.040 MN/mm2
Poisson's ratio = 0.3
Shear Modulus (Shear stress/Strain) = 0.0154 E6 N/mm2
Mass Density = 3.03/103 N-sec2/mm4

With these values the absolute stress magnitude from the teeth models could not be obtained but relative magnitudes and stress directions within a model could be calculated which do not affect the objectives of the work. Though it is not possible to simulate the natural condition of mastication (because in nature, the dentition works in union), while modelling the teeth the natural condition was kept in the mind and hence a vertical load (snow load, Koenigswald et al., 1987) was applied on the cutting edge of the incisors. The load direction was kept parallel to the incisal portion of the curved incisors. The cervical end of the incisors was kept fixed considering that it is anchored in the bone (figs. 1 & 2).

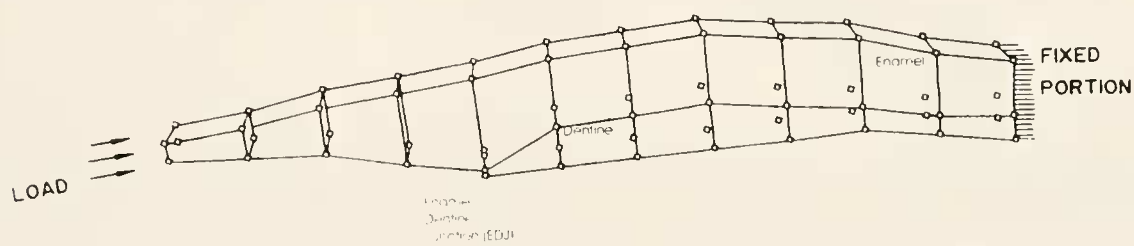

Fig. 2: Finite element model of a rodent incisor. The incisor has been modelled as a series of 3-D hexa elements. While modelling, the natural position of the incisor in the jaw was kept in the mind. One end of the model was kept fixed considering that the cervical end of the incisor is anchored in the bone. A gnawing load was applied parallel to the longer axis of anterior region of the curved incisor.

The load direction was inferred from occlusal features such as striae, notches, vertical pits and surface relief present on teeth, which are formed as a result of various masticatory processes (Greaves, 1973; Rensberger, 1973, 1992; Koenigswald et al., 1987). The resultant tensile stresses were calculated at the centre of the elements using a solver MSC/pal2. The principal tensile stresses were extracted from the result, because a brittle material like dental enamel is weaker under the tensile than the compressive stress and usually fails due to tension (even when the external force is mainly of a compressive nature; Rensberger, 1992). The stress intensities in the models were calculated and plotted (figs 3, 4 & 5). The direction of the maximum tensile stresses were plotted on the model of bars and rodent incisors (figs 6, 7 & 8) and the probable directions of propagation of cracks (perpendicular to the direction of maximum tensile stress at a given point) were determined (figs 9, 10 & 11).

In the present study the absolute magnitude of the stresses in the enamel would be unrealistic, but the study is mainly concerned with the directions of the stresses and these approximate the directions in real teeth. To test this assumption, the long slender curved incisors of recent Guinea Pig and House Rat were loaded in laboratory with the help of Universal Testing Machine (UTM) of 100 kg capacity (the machine is available in Biophysics Laboratory, department of Physics, Nizam College, Hyderabad, India). The limitations of the machine do not allow users to calculate stresses on an object due to pulling load (= wind load, Koenigswald, et al., 1987). For a compressive load analysis the samples were held between two circular jaws in an upright condition with the help of a metallic chuck and load of 1kgf was applied in an interval of time of 1 minute and results were noted (fig. 12). In another case one tooth was subjected to compressive load along the shorter axis of tooth also i.e. in the transverse direction.

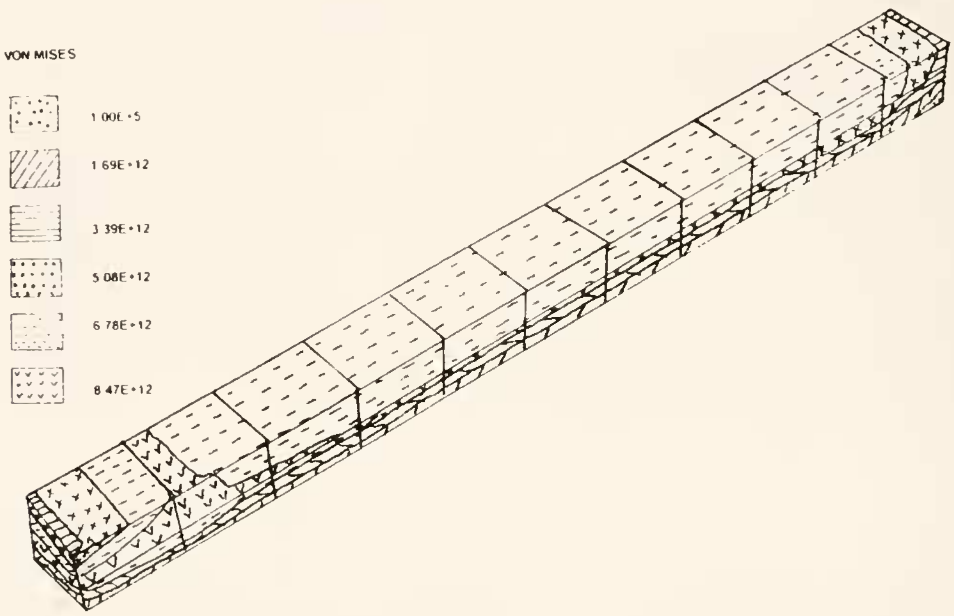

Fig. 3: Finite element model of a double layered straight bar showing stress intensities as observed under the gnawing load condition.

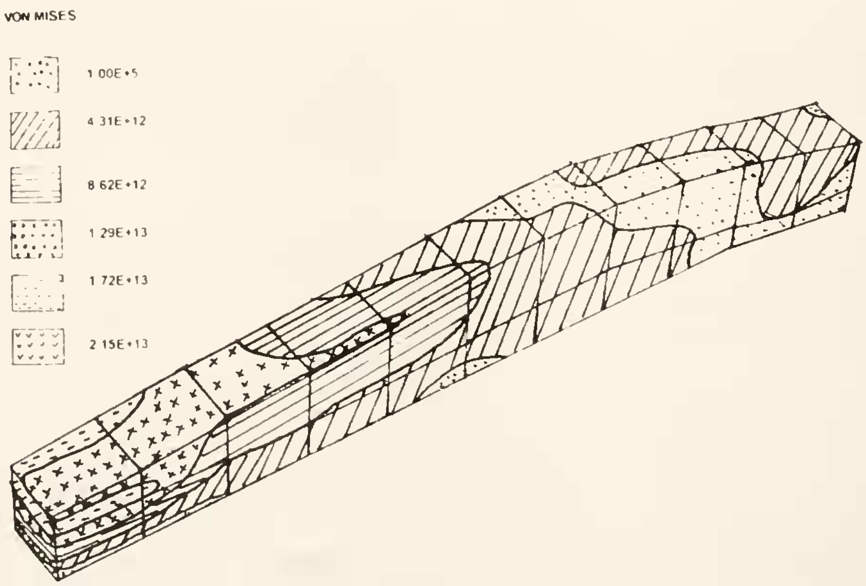

Fig. 4: Finite element model of a double layered curved bar showing stress intensities as observed under the gnawing load condition.

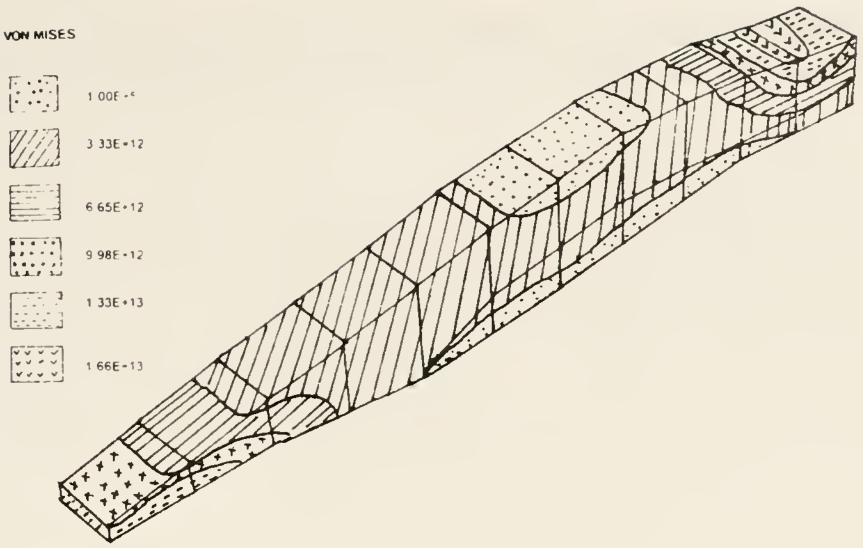

Fig. 5: Finite element model of the curved chisel shaped rodent incisor showing stress intensities as observed under the gnawing load condition. Note the higher magnitude of stresses which are concentrated around the fixed end, thus makes the structure most withstanding against the stresses.

The theoretical results of FEA and laboratory results of UTM were compared with the empirical evidence of stresses in the actual teeth. Rodent incisors of recent age were examined for premortem cracks under the assumption that premortem cracks were caused by gnawing load. The cracks with rounded edges and vertical hairline cracks were identified as of premortem origin (Rensberger, 1987).

Finally, the crack directions in the rodent incisors were compared with their enamel ultrastructure observed under the SEM.

Observations

S E M Study:

Scanning electron micrographs of longitudinally sectioned enamels show distribution of the Hunter Schreger Bands (HSBs), in all the three types of rodent incisor enamel at different orientation. The outer enamel possesses more or less the same structure in all the types of enamel pattern, though the thickness is highly variable. It consists of radial enamel in which prisms rise incisally towards the outer surface of the incisor. The inner enamel consists of longitudinally and transversely sectioned HSBs. The prisms of alternate bands possess the same orientation and are at high angle with the neighbouring bands. Different types of enamel structures observed in the studied incisors are described below:

Pauciserial Enamel (Figs. 13 & 14):

The longitudinally sectioned incisors of ctenodactyloid rodents possess 2 - 6 prisms wide HSBs. The prisms of the outer enamel have relatively low inclination (25°- 55°) and are arranged parallel to or at a very shallow angle to the EDJ (Martin, 1993). The fibres of the Inter Prismatic Matrix (IPM) in the outer enamel envelope the prisms and make a high angle or run perpendicular to the outer enamel prisms and EDJ. The fibres of prisms are more compactly arranged as compared to the fibres of IPM (Keil, 1966).

In the inner enamel of the pauciserial type, it is very difficult to differentiate IPM from prisms because the IPM fibres possess the same orientation which is generally perpendicular to the EDJ, as do the HSB prisms. The orientation of the prisms changes abruptly from one band to other and no transition zone could be demarcated. The HSBs are nearly perpendicular to the

EDJ. The HSB boundary is clearly distinguished and a prism decussation is evident where adjacent, ascending prisms intersect the plane of section. An irregular bifurcation of HSBs is frequent.

Multiserial Enamel (figs. 15 & 16)

In the longitudinal section of the incisors of recent *Cavia porcellus* (Guinea Pig), it was observed that the outer enamel prisms are steeply inclined (up to 80°) and laterally flattened (Martin, 1993). The HSB width usually varies between four and seven prisms. It was observed that the IPM is more clearly displayed in the outer enamel and is perpendicular to the EDJ. The HSBs are incisally inclined at a shallow angle. The prisms have slightly steeper inclination than the HSBs and therefore are forced to bend from one to the next higher HSB. The HSBs are of uniform thickness unlike the pauciserial type. Occasional branching of the HSBs as in the pauciserial is also seen in the multiserial type of enamel.

Uniserial Enamel (figs. 17, 18, 19, 20):

The longitudinal sections of the Incisors of murid rodents and house mouse suggest that the inner enamel is consisting of one prism thick HSBs. The outer enamel prisms are more laterally flattened (Martin, 1993). The HSBs are more incisally inclined in comparison to those in the multiserial enamel. The prisms of one band decussate into the next higher band. In the inner enamel, the IPM is turned perpendicular to the HSBs. No branching was observed in the HSBs of the uniserial enamel.

Finite Element Analysis (FEA):

FEA of simple straight two layered beam/bar (layers are differentiated on the basis of Moduli and Poisson ratio values of enamel and dentine) suggests that when gnawing load is applied on the enamel portion, stresses of higher magnitude are noticed in the whole enamel with the highest value near the point of the load application. The dentine experiences the stresses of comparatively lower magnitude. The whole of the enamel is found to be under compression excepting a small incisal portion where tensile stresses in Z direction (direction of enamel thickness) are noticed. The angle of stresses is found to be cervically inclined from the EDJ.

The FEA of a curved beam suggest that when gnawing load is applied on the enamel portion, the stresses of higher magnitude are noticed in a very small portion at EDJ near the point of the load application. Most of the enamel experiences stresses of lower magnitude when compared with the stress data in simple straight two layered beam. The magnitude of stresses decreases as we go in the cervical direction. The area near the point of load application and cervical end are found to be under compression. In the enamel, the tensile stresses are noticed mainly in Y and Z directions. The inclination of tensile stresses is found to be vertical from the EDJ.

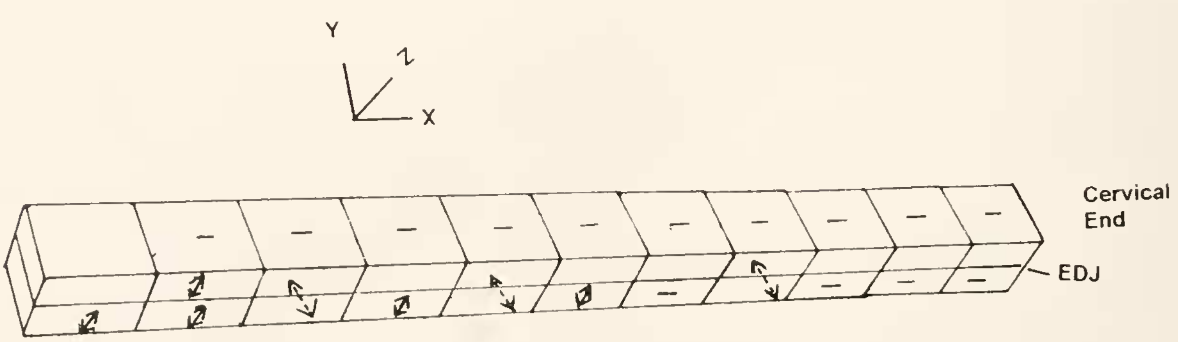

Fig. 6: Finite element model of a double layered straight bar showing direction of the maximum principal stresses as observed under the gnawing load condition.

The FEA of chisel shaped incisors as noticed in rodents, suggests that under a gnawing load condition, the stresses of higher magnitude are noticed in a small lower portion of the enamel at the cutting edge. Most of the stresses of higher magnitude are found to be located near the cervical end anchored in the bone. Major portions of the enamel experiences stresses of the lowest magnitudes when compared with the straight simple and curved beam. The least value of the stresses were noticed in the middle of the incisor enamel. Under gnawing load the major portion of the incisor enamel is found to be under tension except the regions near the point of the load application and the cervical end. The tensile stresses are noticed in Y and Z directions, i.e. in the directions of the enamel width and the thickness. The tensile stresses are found to be incisally inclined from the EDJ (figs. 6, 7 & 8)

In all the above cases a shearing movement along the enamel-dentine junctions is also noticed.

From the direction of the tensile stresses, the most probable direction of the failure was inferred which was found to be nearly vertical along the longer axis of the teeth (figs. 9, 10 &11).

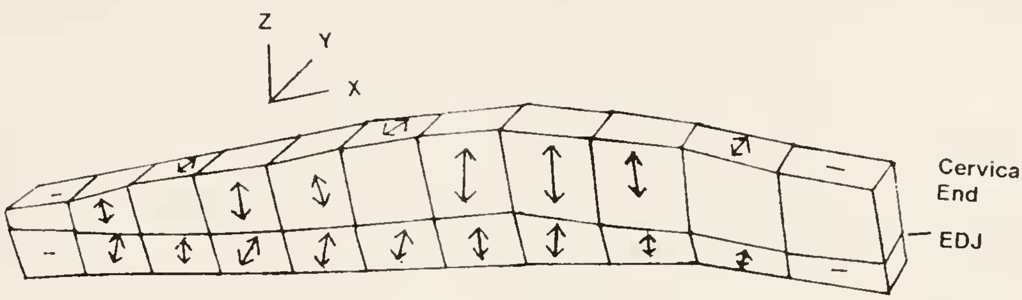

Fig. 7: Finite element model of a double layered curved bar showing direction of the maximum principal stresses as observed under the gnawing load condition

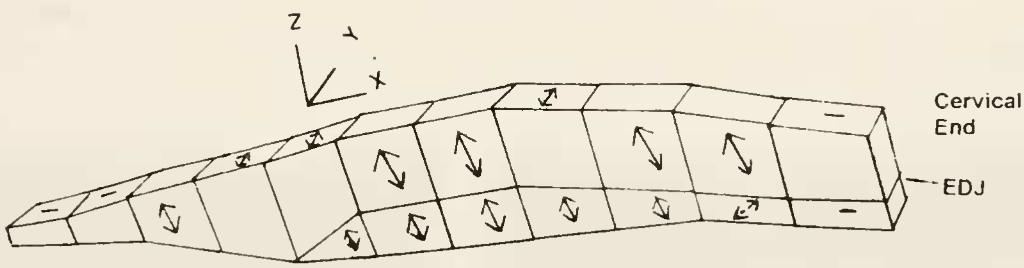

Fig. 8: Finite element model of the curved chisel shaped rodent incisor showing direction of maximum principal stresses as observed under the gnawing load condition.

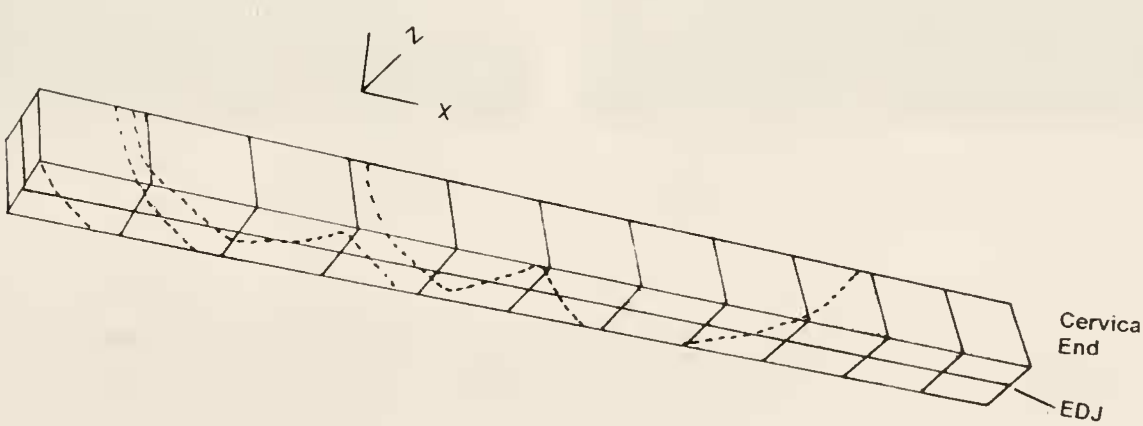

Fig. 9: Double layered straight bar showing direction of the cracks as inferred from the direction of maximum tensile stresses produced due to the gnawing load.

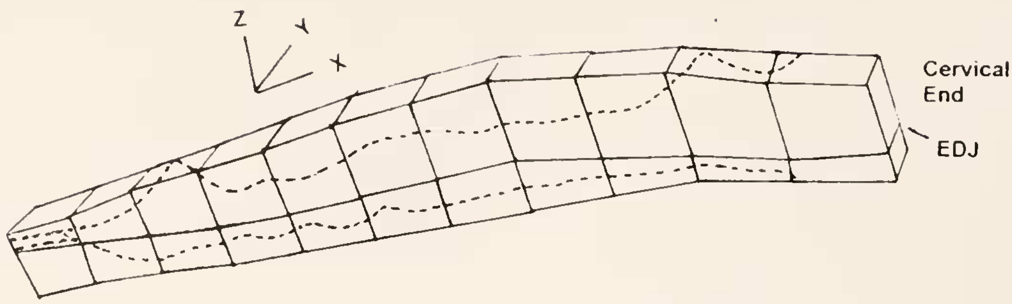

Fig. 10: Double layered curved bar showing direction of the cracks as inferred from the direction of the maximum tensile stresses produced due to the gnawing load.

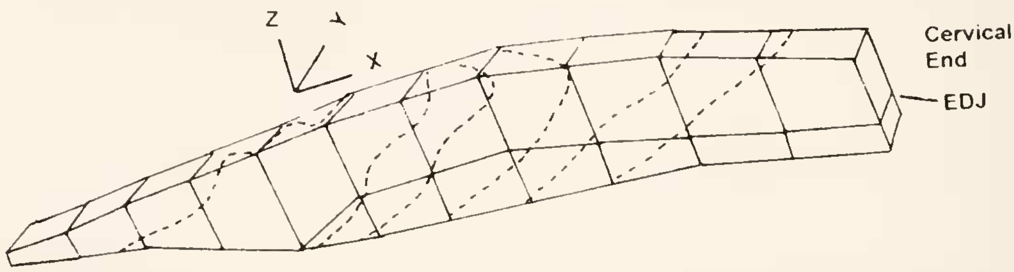

Fig. 11: Curved chisel shaped incisor showing direction of the cracks as inferred from the direction of maximum tensile stresses produced due to the gnawing load.

The UTM analysis suggests that when incisors of rodents are placed under an increasing vertical load condition, the failure of the tooth takes place. The cracks start appearing from apex to base in all the teeth (in static load condition cracks start appearing from base to apex, Rensberger, 1987). In rodent incisors the cracks appear along the longer axis of teeth (fig. 12). The failure of incisors along the EDJ is also noticed.

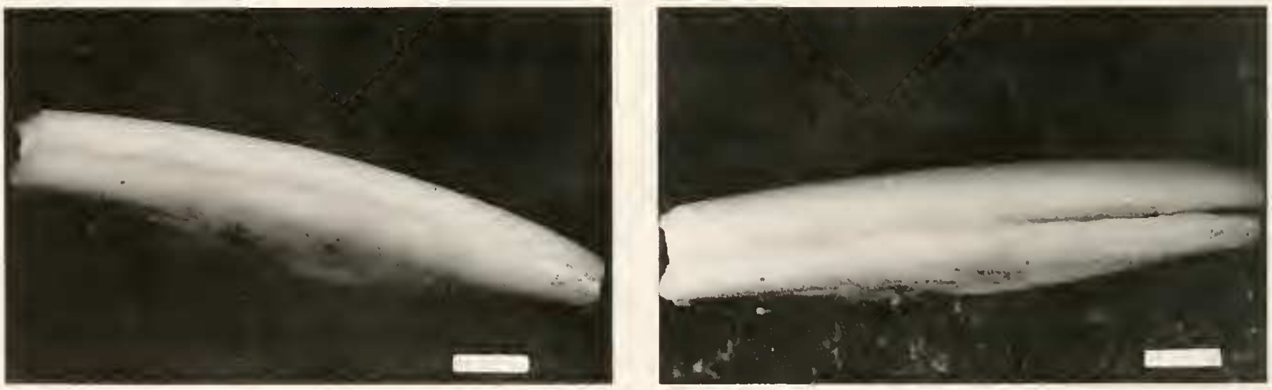

Fig. 12: Rodent incisor (Guinea Pig) subjected to a vertical load parallel to the anterior part of the tooth (gnawing load) with the help of Universal Testing Machine (UTM). The vertical cracks were observed confirming the presence of the stresses as observed in FEA analysis (scale bar = 1 mm).

In the case of the compressive load analysis along the shorter axis of the teeth, i.e. in the transverse direction, the tooth breaks into pieces just in a single loading of 1kgf.

Results and Conclusions

Results of SEM Study:

The structure of the enamel observed under SEM and the direction of the failure observed by FEA, UTM were compared. The results indicate that the inferred cracks' directions in the FE models were similar to the cracks produced in the teeth in laboratory experiments. These cracks are best stopped by the uniserial pattern, present in the incisor enamel of rodents of Oligocene - recent age.

Results of enamel structure in studied rodent incisors indicate that the pauciserial pattern shows a very irregular arrangement of the HSBs and is most generalised in comparison to the multiserial and the uniserial (Sahni, 1980; Martin, 1993). This hypothesis is based on the stratigraphic position of horizons yielding ctenodactyloid rodents and also on the inclination and orientation of the HSBs and the Inter Prismatic Matrix (IPM). As observed in the pauciserial, the IPM in the inner enamel is oriented in the direction of prisms orientation, and it is a primitive condition (Martin, 1990a, 1990b, 1993). Whereas it makes an angle with the prisms in the inner enamel of the multiserial enamel. In uniserial enamel, the IPM crystallites are at right angle to the HSB prisms, strengthening the enamel in the third dimension (Koenigswald & Clemens, 1992; Martin, 1993).

The development of the pauciserial type of enamel pattern in rodents of Eocene age and its gradual change into the multiserial and the uniserial type in the later and recent genera suggests that the change from pauciserial to uniserial through multiserial is an evolutionary feature (Sahni, 1980; Martin, 1993). Earlier to this Koenigswald (1980) argued that multiserial is more primitive than pauciserial, without considering the orientation of IPM crystallites but later this hypothesis was rejected (Koenigswald, 1990, 1992; Martin, 1990a, 1990b, 1993).

Results of Finite Element Analysis:

The results of FE analysis of double layered straight beam, curved beam and chisel shaped incisors suggest that at gnawing load conditions, stresses of maximum magnitude are produced in the enamel region of the straight beam in comparison to the curved beam and the chisel shaped incisors. Straight beam has been found to be the least stable at the gnawing load conditions. In curved beam stresses of high magnitude in the whole enamel and the maximum magnitude on the cutting edge make the structure less effective for the defined purposes. On the other hand, blunt incisal end decreases the efficiency of cutting and gnawing. Whereas in the chisel shaped incisors concentration of high magnitude of stresses in the cervical region make the structure most stable and the sharp cutting edge increases efficiency under the gnawing load conditions. The stresses in the cervical region are dissipated into the jaw bones from where incisors erupt.

The incisally inclined tensile stresses in Y and Z directions of enamel in chisel shaped incisors are more harmful as they may be responsible for the development of the cracks perpendicular to the direction of the stresses (figs. 9, 10 & 11).

Results of Laboratory Experiments:

The Universal Testing Machine (UTM) was found to be very useful in simulating the natural condition of teeth in jaw and applying pressure from different angle. The results of UTM corresponds to the FEA results. By applying increasing load of 1kgf on the cutting edge of rodent incisors, the vertical cracks were observed running along the longer axis of teeth.

The FEA results, UTM results were found to be consistent with the premortem cracks, which tend to have vertical orientation.

In rodents, the incisors keep on growing and enamel once mineralized can not be rebuilt according to the stresses, hence all the functional adaptations have to be produced in the genome, which leads to the uniformity of the enamel microstructure throughout the length of the incisor in any time span (KOENIGSWALD & PFRETZSCHNER, 1991). The microstructure thus generated would be according to the direction of the maximum tensile stresses present in the enamel.

The microstructure of the outer enamel in all the types of rodent incisor enamel is similar and has remained unchanged with time excepting minor changes in the inclination of enamel prisms. During gnawing activity lot of wear stresses are produced in the incisors and the outer enamel provides the best reinforcement against wear (RENSBERGER & KOENIGSWALD, 1980; FORTELIUS, 1984, 1985), because the enamel prisms are oriented parallel to the direction of the load. Probably, this is the reason for the presence of only outer enamel at the cutting edge where maximum wear and abrasion takes place.

In the inner enamel of the pauciserial type, the reinforcement against the incisally inclined tensile stresses in Y and Z directions (the direction of the enamel width and the thickness) is very less, because, the HSBs make an angle with the stress direction (fig. 13). It has been noticed

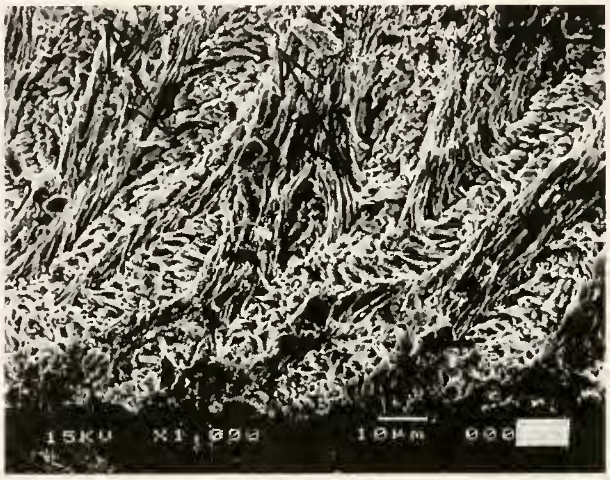

Fig. 13: Pauciserial arrangement of the enamel as observed in a longitudinal section of the incisor enamel of a ctenodactyloid rodent, showing distribution of Hunter Schreger Bands (HSBs). Arrow marks the direction of the maximum tensile stresses observed in the rodent incisor enamel under the gnawing load condition (scale bar = 10 microns). Anterior part (incisal direction) of the incisor is towards the left side of the photograph. Slightly inclined section of the incisor giving an impression of inclined HSBs.

Fig. 14: Longitudinal section of the incisor enamel of a ctenodactyloid rodent, showing arrangement of the prisms in HSBs (scale bar = 10 microns). Anterior part (incisal direction) of the incisor is towards the left side of the photograph.. Slightly inclined section of the incisor giving an impression of inclined HSBs.

that when tensile stresses are at an angle to the HSBs, the cracks thus produced make a low angle with the HSBs and it is the most critical condition (PFRETZSCHNER, 1988; KOENIGSWALD & PFRETZSCHNER, 1991). Since the HSBs are irregular (2-6 prisms wide), the cracks may travel a longer distance in HSBs. The IPM crystallites are also arranged parallel to the HSB prisms, hence provide no reinforcement against such cracks. These cracks are either deflected or stopped only when they reach the point of bifurcation of the bands. In this condition, cracks may damage maximum part of the enamel (KOENIGSWALD et al., 1987).

In the multiserial enamel, the reinforcement against the incisally inclined tensile stresses in Y and Z directions, is much more than in the pauciserial. In the multiserial enamel, the and HSBs are also incisally inclined. The tensile stresses make a very low angle with the HSBs (fig. 15) and thus produce cracks making a high angle with the HSBs. The IPM crystallites make a high angle with HSB prisms, protecting the enamel in the third dimension. This arrangement makes the structure stable under the gnawing load conditions. Since the bands are inclined at a very shallow angle, the structure may be unstable if cracks appear making a low angle with the HSBs. In this condition the crack will travel throughout the HSB (which is 4-7 prisms wide) until it meets a decussating band or it reaches to the point of band bifurcation, and thus it damages a greater part of the enamel.

Fig. 15: Multiserial arrangement of enamel as observed in the longitudinal section of the incisor enamel of *Cavia porcellus* (Guinea Pig), showing distribution of the HSBs and the outer enamel. Arrow marks the direction of the maximum tensile stresses observed in the rodent incisor enamel under the gnawing load condition. Scale bar = 10 microns. Anterior part (incisal direction) of the incisor is towards the right side of the photograph.

Fig. 16: Longitudinal section of a highly etched incisor enamel of *Cavia porcellus* (Guinea Pig), showing arrangement of the outer enamel prisms and the Inter Prismatic Matrix (IPM). Scale bar = 5 microns. Anterior part (incisal direction) of the incisor is towards the right side of the photograph.

In the uniserial enamel the best reinforcement against the incisally inclined tensile stresses in Y and Z directions, has been noticed. The incisally inclined HSBs are almost parallel to the tensile stresses (fig. 18). The cracks, thus produced are oriented almost at the right angle to the HSBs. The orientation of the IPM crystallites prevents failures in the third dimension and makes the structure stable in all the three orthogonal directions (KOENIGSWALD, 1990). This structure is stable even if cracks appear at low angle with the HSBs. In this condition, the IPM and the single prism wide HSBs will soon transmit the crack into next decussating band where it will stop soon due to change in the original direction of cracks (KOENIGSWALD, et al., 1987).

Fig. 17: Uniserial arrangement of the enamel as observed in a longitudinal section of the incisor enamel of *Mus musculus* (House Rat), showing distribution of the HSBs and the outer enamel. Arrow marks the direction of the maximum tensile stresses observed in the rodent incisor enamel under the gnawing load condition. Scale bar = 10 microns. Anterior part (incisal direction) of the incisor is towards the left side of the photograph.

Fig. 18: Longitudinal section of the incisor enamel of *Mus musculus* (House Rat), showing arrangement of the outer enamel prisms and the Inter Prismatic Matrix (IPM). Scale bar = 5 microns. Anterior part (incisal direction) of the incisor is towards the left side of the photograph.

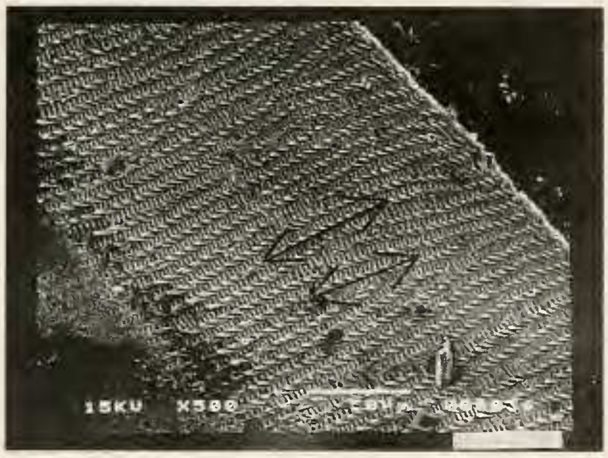

Fig. 19: Uniserial arrangement of the enamel as observed in a longitudinal section of the incisor enamel of a murid rodent, showing distribution of the HSBs. Arrow marks the direction of the maximum tensile stresses observed in the rodent incisor enamel under the gnawing load condition. Scale bar = 50 microns. Anterior part (incisal direction) of the incisor is towards the right side of the photograph.

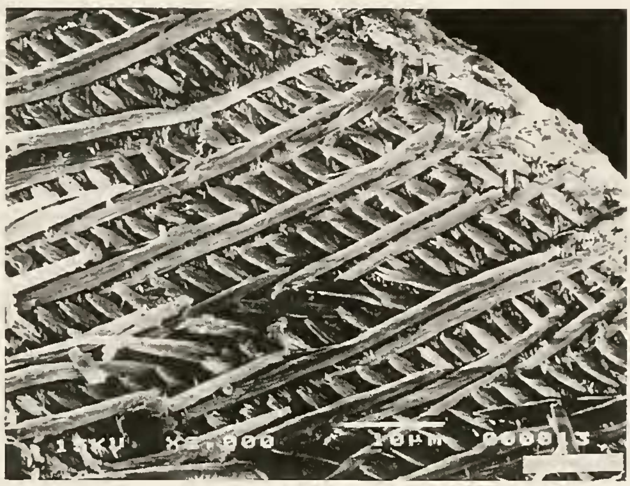

Fig. 20: Longitudinal section of the incisor enamel of a murid rodent, showing arrangement of the prisms in HSBs. Scale bar = 10 microns. Anterior part (incisal direction)of the incisor is towards the left side of the photograph.

Conclusions

From the present study of rodent incisors the following conclusions have been drawn :

1 Curvature of the incisor helps in dissipating the high magnitude of stresses to the cervical end i.e. into the bone from where incisors erupt.

2 In rodent incisors tensile stresses were noticed under gnawing load conditions. The stresses were found to be incisally inclined from EDJ and were oriented mainly in Y and Z directions of the enamel width and the thickness.

3 The changes in the microstructure of rodent incisor enamel of successive ages (from Eocene to recent) are in response to a need for a better reinforced structure against the gnawing stresses.

4 Stress response in all the three types of incisor enamel suggests that the pauciserial type of enamel in comparison to the multiserial and the uniserial, is least effective in stopping incisally inclined stresses produced due to gnawing load condition.

5 The uniserial type of enamel provides the best reinforcement against incisally inclined tensile stresses. Its single prism wide HSBs provide an increased stability against any kind of stresses, in comparison to 4-7 prisms wide HSBs in multiserial enamel.

Acknowledgements

Author is grateful to Prof. Ashok Sahni (CAS in Geology, Panjab Universiy , Chandigarh, India), Dr. S. A. Jafar (Birbal Sahni Institute of Palaeobotany, Lucknow, India) and Prof. H. H. Schleich (Fuhlrott Museum, Wuppertal, Germany) for reading the text and offering valuable suggestions. Dr. Rajeev Patnaik (CAS in Geology, Panjab University, Chandigarh) provided *Mus* dental material for the present study. Dr. Adeel Ahmad (Nizam College, Hyderabad) very kindly provided facilities for the experimental analyses using UTM. Financial assistance provided by Department of Science and Technology, New Delhi under the young scientist scheme (SR/SY/A-09/94) and DAAD, Bonn for post-graduate studies in Wuppertal, Germany, is gratefully acknowledged. Laboratory facilities for the work were provided by the Head, Geology Department, Lucknow University, India and the Director, Fuhlrott Museum, Wuppertal, Germany.

Literature

Boyde, A. (1976): Enamel structure and cavity margins. Operative Dentistry, **1**(1): 13-28.

Boyde, A.; Fortelius, M.; Lester, K.S. & Martin, L. B. (1988): Basis of the structure and development of mammalian enamel as seen by scanning electron microscopy. Scanning Microscopy, **2**: 1479-1490.

Flynn, L.J.; Nevo, E. & Heth, G. (1987): Incisor enamel microstructure in blind mole rats: Adaptive and phylogenetic significance. Journ. Mammology, (3): 500-507.

Fortelius, M. (1984): Vertical decussation of enamel prisms in lophodont ungulates. In: Fearnhead, R.W. & Suga, S. (eds.): Tooth Enamel, IV: 427-431; Amsterdam (Elsevier).

Fortelius, M. (1985): Ungulate cheek teeth: developmental, functional and evolutionary interrelations. Acta Zoologica Fennica, **180**: 1-76.

Greaves, W.S. (1973): The inference of jaw motion from tooth wear facets. Journ. Paleontol., **47**: 1000-1001.

Keil, A. (1966): Grundzüge der Odontologie. 2, Aufl., Berlin (Borntraeger).

Koenigswald, W. v. (1980): Schmelzmuster and morphology in the molars of Arvicolidae (Rodentia). Abh. Senckenb. Naturforsch. Ges., **539**: 1-129.

Koenigswald, W. v. (1985): Evolutionary trends in the enamel of rodent incisors. In : Luckett W.P., Hartenberger, J. L. (eds): Evolutionary Relationships among Rodents: A Multidisciplinary Analysis. NATO ASI Ser. A Life Sciences, **92**: 403-422; New York (Plenum Press).

Koenigswald, W. v. (1990): Ein ungewöhnliches Schmelzmuster in den Schneidezähnen von *Marmota* (Rodentia, Mammalia). N. Jb. Geol. Paläont., Abh. **190**: 53-73.

Koenigswald, W. v. (1992): Tooth enamel of cave bear (*Ursus spelaeus*) and relationship between diet and enamel structures. In: Forsten, A., Fortelius, M., & Werdelin L. (eds.): Memorial vol. Björn Kurtén, Annales Zool. Fennica.

Koenigswald, W. v. & Clemens, W. A. (1992): Levels of complexity in the microstructure of mammalian enamel and their application in studies of systematics. Scan. Microscopy, **6**: 195-218.

Koenigswald, W. v. & Pfretzschner, H. U. (1991): Biomechanics in the enamel of mammalian teeth. In: Schmidt-Kittler, N. & Vogel, K. (eds.): Constructional Morphology and Evolution: 113-125; Berlin, Heidelberg (Springer).

Koenigswald, W. v.; Rensberger, J. M. & Pfretzschner, H. U. (1987): Changes in the tooth enamel of early Paleocene mammals allowing increased diet diversity. Nature, **328**: 150-152.

Korvenkontio, V. A. (1934). Mikroskopische Untersuchungen an Nagerincisiven, und Hinweise auf die Schmelzstruktur der Backenzähne. Annales zoologici societatis Zoologicae.- Botanicae. Fennicae. Vanamo., i-xiv, 1-274.

Martin, T. (1990a): Herkunft der caviomorpen Nagetiere Südamerikas: Hinweise aus dem Inzisiven-Schmelz. Nachr. Dt. Geol. Ges, **43**: 61-62.

Martin, T. (1990b): Schmelzstruktur in den Inzisiven alt und neuweltlicher hystricognather Nagetiere. Palaeovertebrata, Memoir, Extra : 1-168.

Martin, T. (1993): Early rodent Incisor Enamel Evolution: Phylogenetic Implications. Journ. Mammal. Evol., **1**: 227-254.

MARX, A. (1995): Analysis of masticatory stresses in hypsodont molars of herbivores by finite element modelling. In: J. MOGGI-CECCHI (ed.): Aspects of Dental Biology: 129-146.
PFRETZSCHNER, H. U. (1988): Structural reinforcement and crack propagation in enamel. In: RUSSELL, D. E. et al.(eds): Mem. Mus. Natn. Hist. Nat., Paris, **53**: 133-143.
PFRETZSCHNER, H. U. (1992): Enamel microstructure and hyposodonty in large mammals. In: P.SMITH & E. TCHERNOV (eds.): Structure, Function and Evolution of Teeth.: 147-162; London and Tel Aviv (Freund Publishing House).
PFRETZSCHNER, H. U. (1994): Biomechanik der Schmelzmikrostruktur in den Backenzähnen von Großsäugern. Palaeontographica, **234**: 1-169.
RENSBERGER, J. M. (1973): An occlusion model for mastication and dental wear in herbivorous mammals. Journ. Paleontol., **47**: 515-528.
RENSBERGER, J. M. (1987): Cracks in fossil enamels resulting from premortem vs. postmortem events. Scan. Microscopy, **1**: 631-645.
RENSBERGER, J. M. (1992): Relationship of chewing stress and enamel microstructure in rhinocerotoid cheek teeth. In: P. SMITH et al. (eds.): Structure, Function and Evolution of Teeth: 163-183.
RENSBERGER, J. M. (1993): Adaptation of enamel microstructure to differences in stress intensity in the Eocene perissodactyl *Hyracotherium*. In: I. KOBAYASHI et al. (eds.): Struc. For. Evol. Fossil Hard Tissues: 131-145.
RENSBERGER, J. M. (1995a): Determination of stresses in mammalian dental enamel and their relevance to the interpretation of feeding behaviours in extinct taxa. In: J. THOMASON (ed.): Funct. Morphol. Verteb. Paleont.: 151-172.
RENSBERGER, J. M. (1995b): Relationship of chewing stresses to 3-D geometry of enamel microstructure in rhinocerotoids. In: J. MOGGI-CECCHI (ed.): Aspects of Dental Biology: 129-146.
RENSBERGER, J. M. & KOENIGSWALD, W. v. (1980): Functional and phylogenetic interpretation of enamel microstructure in rhinoceroses. Paleobiology, **10**: 439-452.
RENSBERGER, J. M. & PFRETZSCHNER, H. U. (1992): Enamel structure in astrapotheres and its functional implications. Scan. Microscopy, **6**: 495-510.
SAHNI, A. (1980). SEM studies of Eocene and Siwalik rodent enamels. Geoscience Journ,. **1** (2): 21-30.
WAHLERT, J. H. (1989): The three types of incisor enamel in rodents. In: BLACK C. C. & DAWSON, M. R. (eds.). Papers on fossil rodents in honour of A. E. Wood. Science Series Natural History Museum of Los Angeles County, **33**: 7-16.
WATERS, N. E. (1980): Some mechanical and physical properties of teeth. In: Symposia of the society for experimental Biology **34**, The mechanical properties of biologic materials: 99-135; Cambridge (CambridgeUniversity Press).